

Fine Structure of the Tentacles of *Phoronis australis* Haswell (Phoronida, Lophophorata)

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Abstract

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The epidermis of the tentacles of *Phoronis australis* consists of six cell types: supporting cells, choanocyte-like sensory cells, both types monociliated, secretory A-cells with a mucous secretion, and three kinds of B-cells with mucoprotein secretions. On cross-sections of the tentacle, one can distinguish four faces: the frontal one, heavily ciliated and located between the two frontolateral rows of sensory cells, the lateral and the abfrontal ones. The orientation of the basal structures of the cilia is related to the direction of their beat. The basiepidermal nervous system is grouped mainly at the frontal and abfrontal faces. The basement membrane is thickest on the frontal face and consists of circular collagen fibrils near the epidermis and longitudinal ones near the peritoneum. All peritoneal cells surrounding the mesocoel are provided with smooth longitudinal myofibrils, and isolated axons are situated between these cells and the basement membrane. The wall of the single blood capillary in each tentacle consists of epitheliomuscular cells with circular myofilaments, lying on a thin internal basal lamina; there is no endothelium.

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Introduction

The lophophore in Phoronida has a feeding, respiratory, and protective function (Hyman 1959; Emig 1976). Its general structure and its function in feeding are rather well known (see Strathmann 1973, 1982; Emig, 1976, 1982; Gilmour 1978; Johnson 1988), but there is little information about its fine structure.

The lophophore of *Phoronis australis* Haswell, 1883, one of the most complex among the Phoronida, forms a spiral on each side with 2.5–3.5 coils; the 400–1600 tentacles are arranged in a double row (Emig 1979, 1982). The rod-shaped tentacles are rounded rectangular in cross-section with a heavy ciliation on the frontal third and scattered cilia on the abfrontal two-thirds (Figs 1–2). Distally, the frontal and abfrontal faces become indistinguishable and the tip of the tentacle appears uniformly ciliated. The tentacles of the external and internal rows are facing each other by their frontal faces; no difference has been detected between the tentacles of the two rows.

The present ultrastructural and histochemical investigations will focus on the functional morphology of the lophophore in describing its epidermal ciliation, cell types, nervous system, coelomic lining, and blood capillary.

Material and Methods

Adult individuals of *Phoronis australis* were collected from tubes of *Cerianthus* sp. (Anthozoa) from the Mediterranean coast, near Almería (Spain), at 2–3 m depth (September 1987).

After removal from the *Cerianthus* tube, the specimens of *P. australis* were fixed in 4% glutaraldehyde in sea water and post-fixed in 1% osmium tetroxide in sea water. Tissue pieces were dehydrated in acetone, block-stained with 2% uranyl acetate during dehydration, and embedded in Araldite via propylene oxide. The blocks were sectioned with an LKB III ultramicrotome; the sections post-stained in lead citrate were viewed and photographed using a Philips EM 201 electron microscope. Semi-thin sections stained with toluidine blue were used to study the gross morphology.

For SEM, the material was fixed and dehydrated following the same procedures as for TEM. Critical-point dried samples were mounted on metal specimen stubs, sputter-coated with pure gold, and viewed with an ISI SX-25 scanning electron microscope.

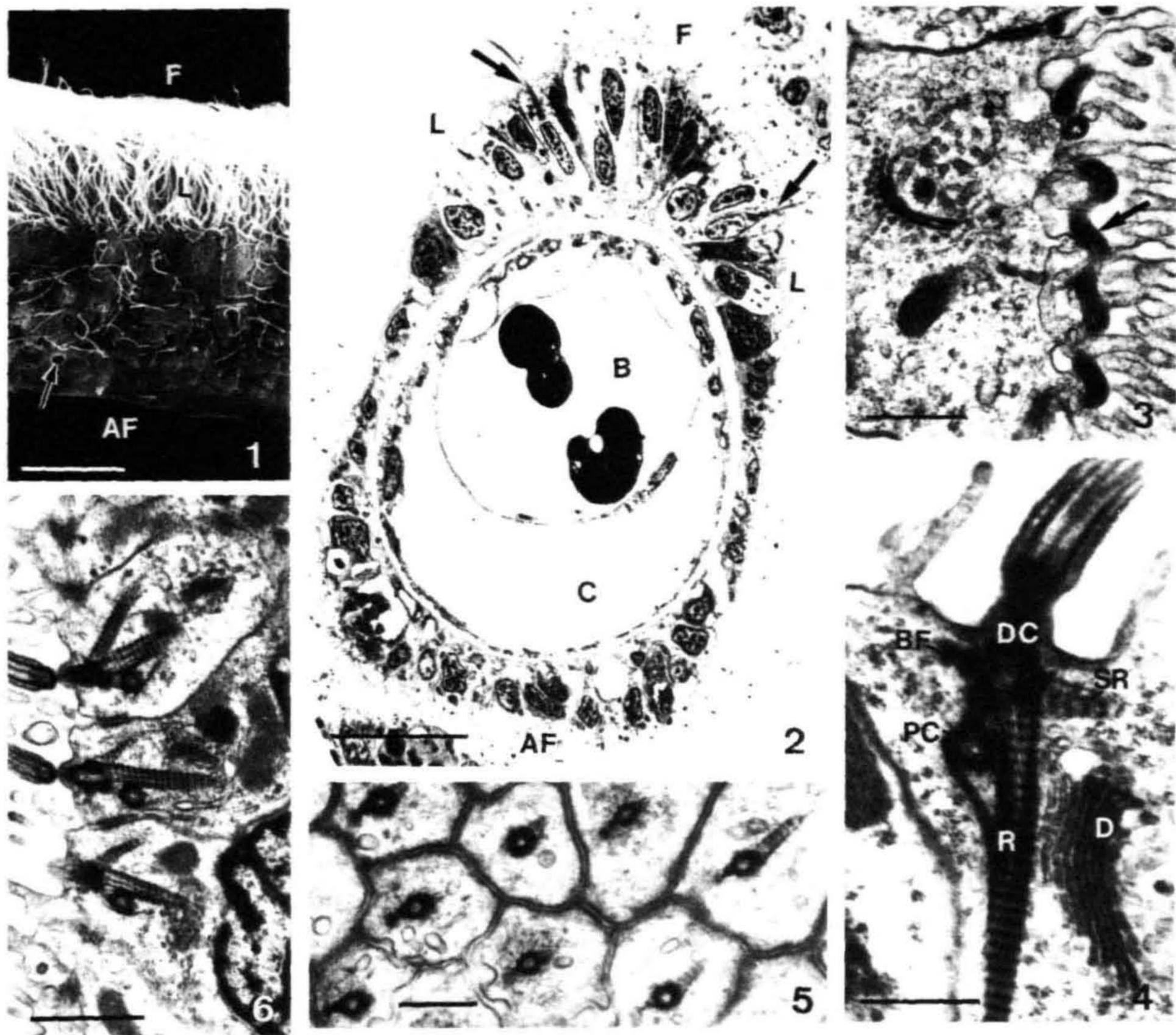
For histochemical tests, the specimens were embedded in paraffin after fixation in neutral formalin or Bouin's fluid. The following histochemical techniques were employed with adequate controls as detailed in Pearse (1968): Periodic acid-Schiff (PAS) after McManus, toluidine blue (TB), alcian blue (AB), and Danielli's tetrazoreaction.

Results

Epidermis

The epidermis of the tentacles is a simple epithelium, with columnar cells on the frontal face, and cuboidal to nearly squamous cells on the abfrontal face (Fig. 2). The secretory cells lack cilia but all the other cell types are monociliated; all cell types have microvilli. Cells undergoing mitosis are often seen, suggesting a proliferation of epidermal cells for tentacular growth and for substitution of dead or damaged cells.

The following six cell types have been distinguished.



Figs 1–6.—*Fig. 1.* SEM micrograph of a tentacle in lateral view showing the strongly ciliated frontal and lateral faces, the sparsely ciliated abfrontal face, and the secretory cell pores (*arrow*). Note the conspicuous limit between lateral and abfrontal faces. Scale bar $17\ \mu\text{m}$.—*Fig. 2.* Transverse section of a tentacle. *Arrows* show the sensory cells. Scale bar $10\ \mu\text{m}$.—*Fig. 3.* Bacteria (*arrow*) lying within the microvillus border on the epidermal cell surface. Scale bar $0.7\ \mu\text{m}$.—*Fig. 4.* Arrangement of the basal structures of the cilium in a supporting epidermal cell. Scale bar $0.4\ \mu\text{m}$.—*Fig. 5.* Tangential section of the epidermis showing the arrangement of the basal foot–secondary rootlet lines; basal feet point to the abfrontal face. Scale bar $0.7\ \mu\text{m}$.—*Fig. 6.* Epidermal cells of the left lateral face of a tentacle; frontal face is towards the top. Scale bar $1\ \mu\text{m}$.

Supporting cells. The term 'supporting cells' is used here to denote epidermal cells which are not specialized as are the secretory or sensory cells. These cells represent the main cell type in the tentacles; they bear most of the epidermal ciliation and have slender microvilli with longitudinal filaments and a dense apex from which tiny radial processes arise to contact adjacent microvilli. A well-developed filamentous glycocalyx covers the cell surface; it appears more electron dense near the apices of the microvilli. Bacteria are often seen among the microvilli or lying on them (Fig. 3). Coated pinocytotic vesicles occur near the bases of the microvilli, sometimes in deep invaginations.

The single cilium, with the usual $9 \times 2 + 2$ pattern, is covered with a glycocalyx. Its basal complex consists of a distal centriole at the base of the axoneme, with a

basal foot, and a more proximal accessory centriole; two rootlets arise from them (Figs 4–6). A dictyosome occurs often close to the main rootlet, under the proximal centriole; it comprises 5–8 flat electron-dense saccules (Fig. 4). The main rootlet runs deeply into the cell perpendicular to the cell surface, while the secondary rootlet lies parallel to the cell surface opposite to the basal foot and the accessory centriole (Figs 4, 6). The complex basal foot/secondary rootlet/accessory centriole shows two orientations around the tentacle: parallel to the long axis of the tentacle with the secondary rootlets on the side adjacent to the tip of the tentacle in frontal and abfrontal cells and perpendicular to this axis with the secondary rootlets towards the frontal face in the lateral cells (Figs 5–7). The rows of the sensory cells described below are situated between the frontal and lateral faces (Figs 2, 7).

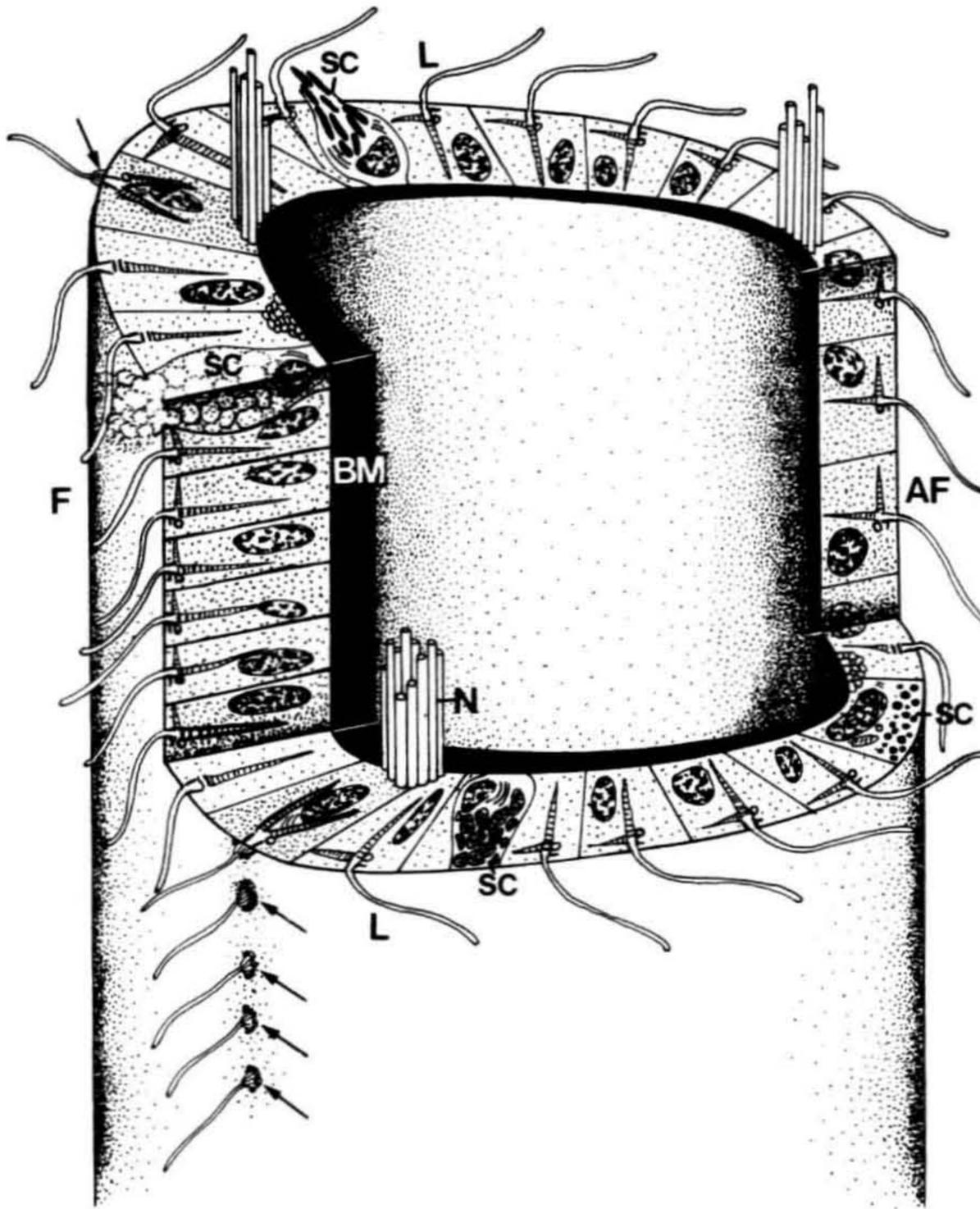


Fig. 7. Diagram of the epidermis of a tentacle showing the four faces and their ciliation with the different beating directions. Cilia are at the end of their effective stroke. Sensory cells are indicated by arrows.

In the cytoplasm, mitochondria with transverse cristae in a dark matrix are abundant as well as free ribosomes (polyribosomes) and dense bodies. Some multivesicular bodies are interpreted as lysosomic stages. Occasional lipid droplets occur in the basal and middle parts of the cell. There is a large heterochromatin-rich nucleus with a prominent nucleolus and numerous ribosomes lying on the nuclear envelope. Coated vesicles are observed at the contact surface of the basal cell membrane with the underlying basement membrane.

On the frontal face the cells are columnar (Fig. 2), distally joined by zonula adherens junctions, and further proximally by long septate junctions. At the abfrontal and lateral faces, the monociliated cells are more flat and broad and their ciliation consequently looks more sparse (Fig. 1, 2); neighbouring cells show deep interdigitations giving additional junctional support.

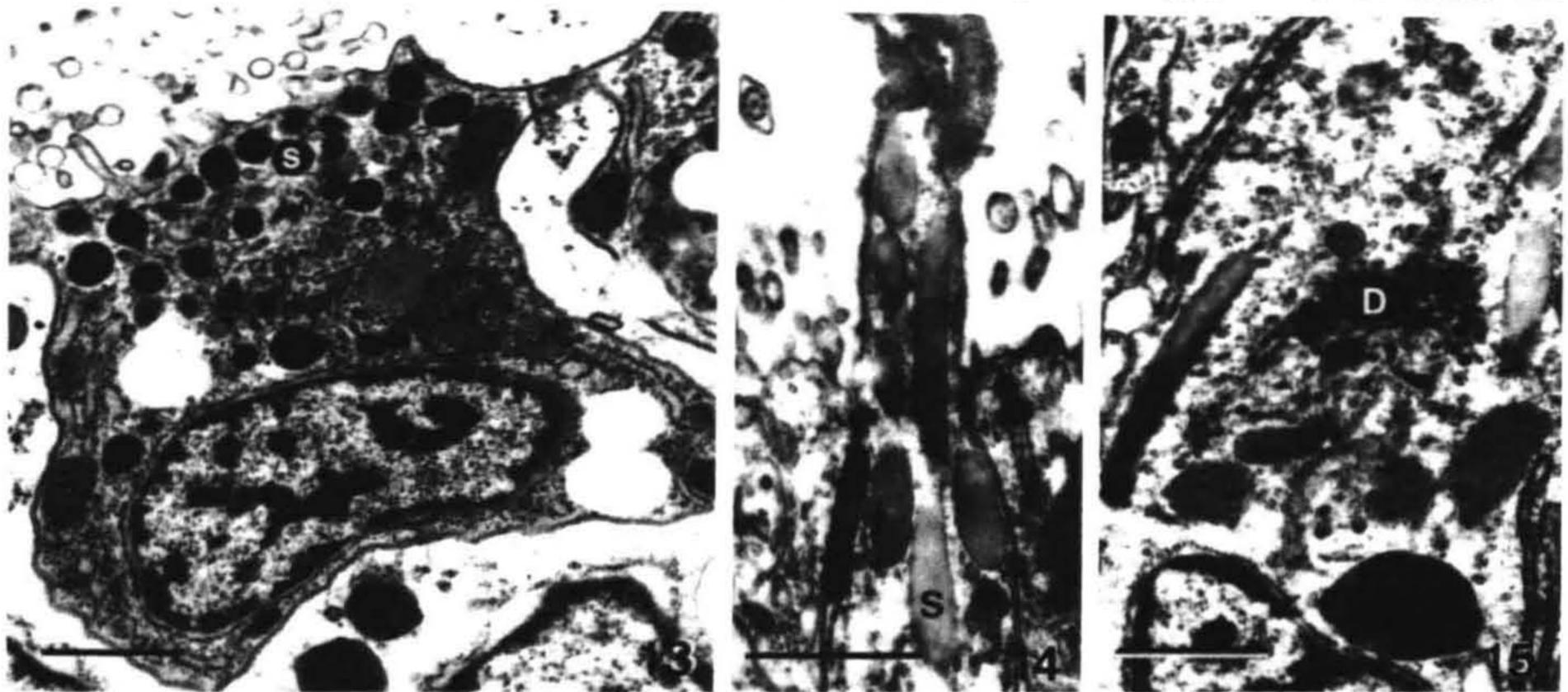
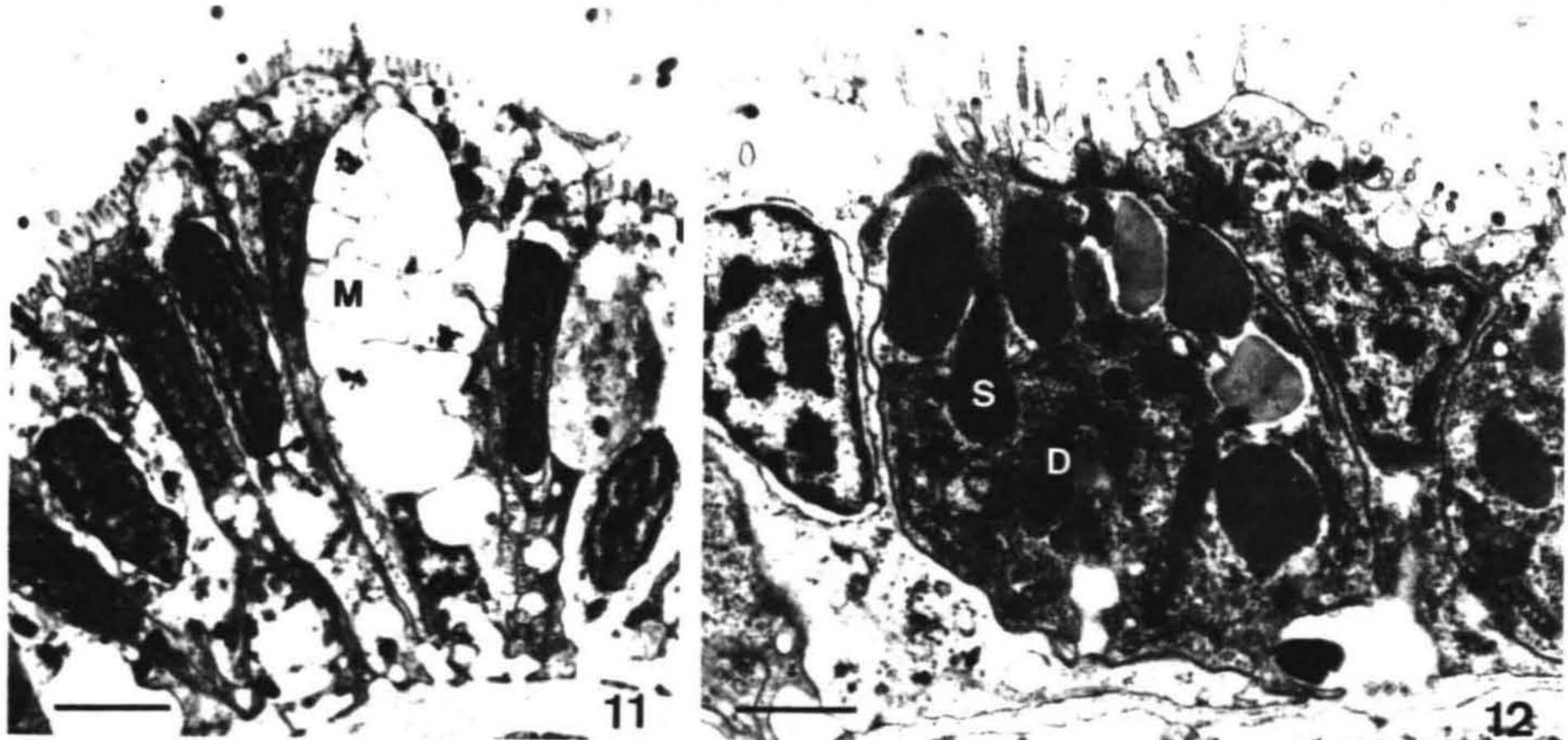
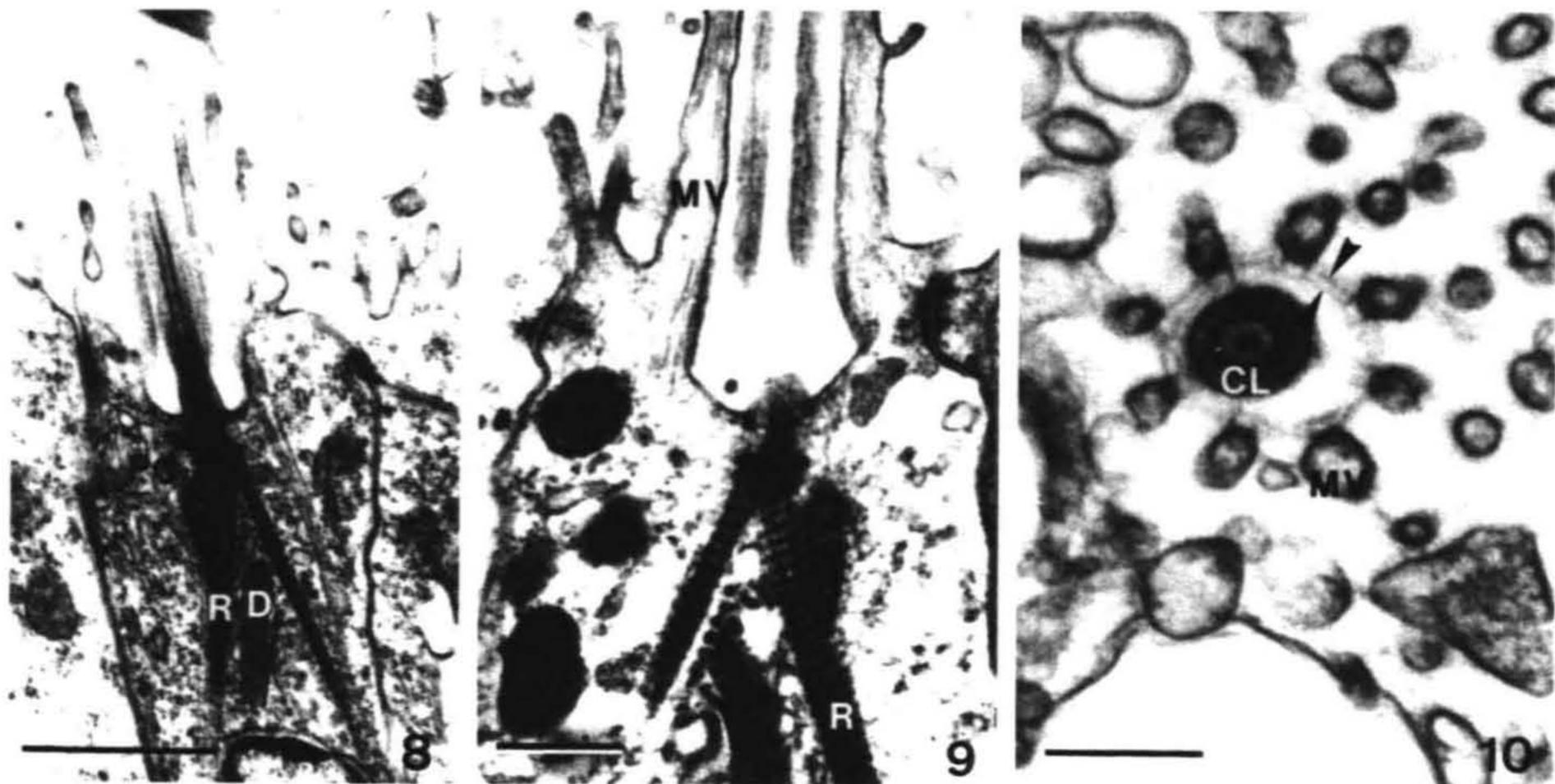
Sensory cells. These cells are arranged in two longitudinal rows along the frontolateral edges (Figs 2, 7); their cilium is surrounded by a crown of eight keel-shaped microvilli (Figs 8–10), which are longer than those of the surrounding supporting cells and contain strong tonofilament bundles deeply rooted into the cell. The inner edge

of the microvilli appears darker than the outer one and extends into the pit towards the cilium; the microvillus apex is electron dense and bears a well-developed glycocalyx, particularly on the inner edges of the crown (Figs 9, 10). In cross-section this inner glycocalyx of the microvilli is seen as tangential, concentric bands with pairs of bridges on every microvillus (Fig. 10). Unlike the basal ciliary structures of the above-described supporting cells, the main and secondary rootlets of the cilium run on each side of the nucleus with the Golgi apparatus lying between them (Figs 8, 9).

The cytoplasm has numerous free ribosomes, endoplasmic reticulum, and mitochondria. The basal part of the sensory cells is in direct contact with the abundant basiepithelial nerve fibres; however, synapse contacts are rare.

Secretory cells. Two main secretory cell types (A and B) can be distinguished by their histochemical reactions and ultrastructural features.

A-cells give a strong metachromatic reaction with toluidine blue, a positive reaction with Alcian blue and a negative one with the PAS and with the tetrazoreaction: they are mucous cells. A large mass of electron-lucent mucus occupies almost the whole cytoplasm (Fig. 11).



The well-developed Golgi apparatus seems to be mainly responsible for the mucus formation; free ribosomes are abundant. This cell type is abundant around the basis of the tentacle and becomes less and less numerous up to the apex.

B-cells stain orthochromatically with toluidine blue; they do not stain with alcian blue but give a positive reaction with the PAS method and with the tetrazoreaction. They secrete mucoproteins, and have a random distribution along the tentacles. According to the ultrastructural features, three kinds of B-cells can be distinguished:

B1-cells (Fig. 12) with large secretory granules, irregular to polygonal in shape, variable in electron density; cytoplasm rich in free ribosomes with peripheral flat cisterns of RER and Golgi apparatus well-developed with dark contents similar to the secretory homogeneous material inside the granules.

B2-cells (Fig. 13) with smaller and darker secretory granules, arising from dilated cisterns of the RER as fibrillar material, and posteriorly elaborated in the Golgi apparatus to form fully developed secretory granules. Light areas in the cytoplasm probably belong to lipid droplets.

B3-cells (Figs 14, 15) secreting elongated rod-like granules, filled by a homogeneous and moderately electron-dense material which is clearly elaborated by a prominent central Golgi apparatus. Small vesicles pinch off the Golgi saccules and release their contents into the growing rod-like granules. Flat cisterns of RER, free ribosomes and multivesicular bodies also occur in the cytoplasm (Fig. 15). When mature, the cell builds up an apical, chimney-like structure through which the granules are released over the microvilli (Fig. 14); the images suggest that they do not lose their shape and aspect immediately after extrusion (Fig. 14). This cell type is less abundant than B1 and B2 cell types. The basal part of these cells is directly associated with nervous fibres, where several synapse-like contacts have been observed.

Basiepidermal nervous system

Two main groups of longitudinal basiepithelial nervous fibres lie directly on the basement membrane, one more conspicuous on the frontal side and another on the abfrontal side of the tentacle (Figs 2, 16). The number of bundles in each group is variable, as well as the number of fibres in each bundle.

The axonal cytoplasm is electron lucent, containing tubules, fibrils, mitochondria, and numerous small,

rounded vesicles which are usually clear, but sometimes dense. Putative synapses between axons have been observed many times but contacts between axons and epidermal cells are rare (Fig. 17).

Basement membrane

Between the epidermis and the peritoneum, there is a thick basement membrane (Figs 2, 16, 18–20). The epidermis and the peritoneum both lie directly on a fine basal lamina under which a thick layer of collagen fibres occurs, embedded in an amorphous and electron-lucent matrix. The fibres closer to the epidermis have a circular arrangement while those closer to the peritoneum follow the long axis of the tentacle (Fig. 18). The basement membrane is thickest at the basis of the tentacle and gradually becomes thinner near the apex. It is thickest at the frontal face of the tentacle, where it supports a taller epidermis (Fig. 2). No cells have been seen passing through this basement membrane.

Coelomic lining

The mesocoelomic cavity, the lumen of the tentacle, is lined by a peritoneal epithelium formed by a continuous layer of squamous, monociliated myoepithelial cells (Figs 2, 19, 20). Peritoneal cells are joined to one another by junctions of the 'zonula adherens' type (Figs 18, 19), and the cell membrane facing the basal lamina has extensive dark areas which may have a junctional function. The structure of the axoneme of the peritoneal cilia was not observed. The myofilaments are parallel to the long axis of the tentacle (Fig. 21); two categories occur: thick filaments, showing a variable diameter, which is perhaps indicative of their spindle-like shape, and thin filaments, surrounding the thicker ones (Figs 21, 22).

A double row of large peritoneal cells, almost filled with myofilaments, lines the junction of the tentacle blood capillary with the main basement membrane (Figs 22, 27, 28). The cells lining the abfrontal side are flatter. The lateral peritoneal cells show a well-developed Golgi apparatus and mitochondria, flat and long cisterns of RER and a small number of myofilaments (Figs 2, 19, 20, 23).

Longitudinal axons run between the peritoneal cells and the basement membrane (Figs 20, 22).

Coelomocytes often occur in the coelomic cavity. Two main types can be distinguished: (1) a globular lymphocyte-like cell type (Fig. 24) with numerous short, blunt pseudopodia, a darker cytoplasm with dense bodies, glycogen areas and a well-developed SER, usually free in the coelomic cavity; (2) an amoebocyte-like cell type (Fig. 25) with few long pseudopodia and showing an electron-lucent cytoplasm with numerous vacuoles is often attached to one another or/and to the coelomic wall.

Blood capillary

Each tentacle has a single blood capillary along the frontal face, almost to the tip (Figs 2, 19, 20).

Figs 8–15.—Fig. 8. Sensory cell showing the single cilium and the particular arrangement of the ciliary rootlets. Scale bar 1 μm .—Fig. 9. Detail of the apical pit of a sensory cell. The microvilli surrounding the cilium bear microfilaments. Scale bar 0.5 μm .—Fig. 10. Cross-section through the choanocyte-like apical structure of a sensory cell. Arrows point to the glycocalyx coat. Scale bar 0.4 μm .—Fig. 11. Secretory A-cell with mucous secretion. Scale bar 2 μm .—Fig. 12. Secretory B1-cell with mucoprotein secretion. Scale bar 1 μm .—Fig. 13. Secretory B2-cell with mucoprotein secretion. Scale bar 1 μm .—Fig. 14. Extrusion of the mucoprotein material of a secretory B3-cell. Scale bar 1 μm .—Fig. 15. Middle part of B3-cell showing the formation process of a secretion granule. Note the Golgi vesicles with a growing granule. Scale bar 1 μm .



Figs 16–19.—Fig. 16. Basiepithelial bundles of nerve fibres in the abfrontal face. Scale bar 1 μm .—Fig. 17. High magnification of a group of nerve fibres on the abfrontal face with a possible synapsis site (arrow). Scale bar 0.2 μm .—Fig. 18. Basement membrane showing the two distinct layers of perpendicularly directed collagen fibres between the epidermis and the peritoneum. Scale bar 0.5 μm .—Fig. 19. Longitudinal section of a tentacle showing its internal organization. Scale bar 5 μm .

The capillary is a longitudinal infolding of the peritoneum and its basement membrane; it has no endothelial lining (Figs 25–27). These peritoneal cells are also monocoliated, but their myofilament bundles are arranged transversally around the capillary (Figs 20, 26, 27). The basal lamina of the capillary wall is continuous with the base-

ment membrane of the tentacle along the attachment line of the vessel (Fig. 28).

The capillary has been observed both in the contracted and the relaxed state (Fig. 20). When relaxed, it is nearly circular in cross-section, and occupies a large part of the coelomic lumen (Figs 2, 19). When contracted, it is much

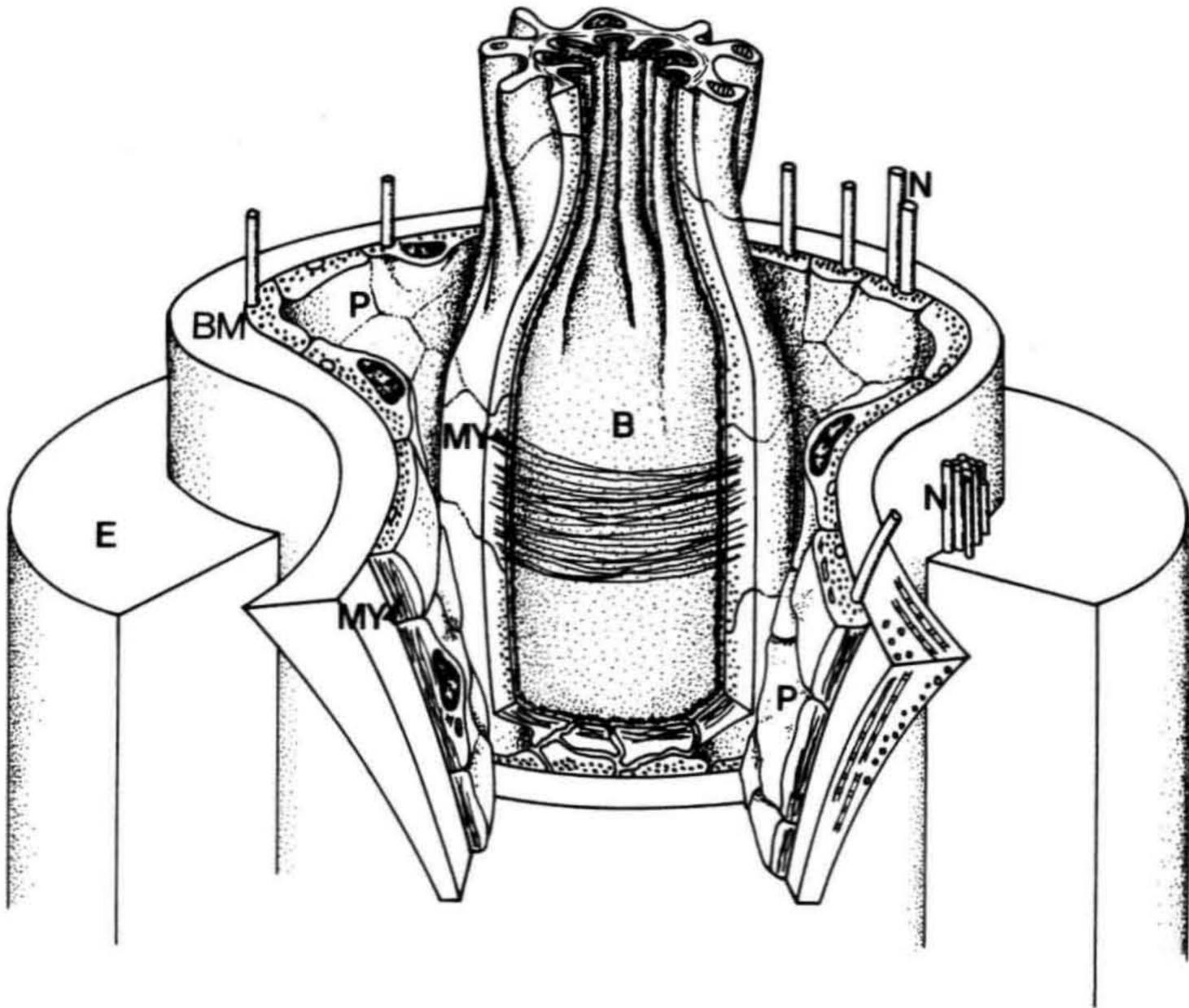


Fig. 20. Diagram of the internal organization of a tentacle, viewed from the opened frontal side. The blood capillary is drawn contracted at the top and relaxed at the bottom.

narrower, and both the inner and the outer linings of the capillary and the basal lamina are thrown into deep longitudinal folds; 'dense bodies' may be seen in the myofibril bundles (Fig. 27).

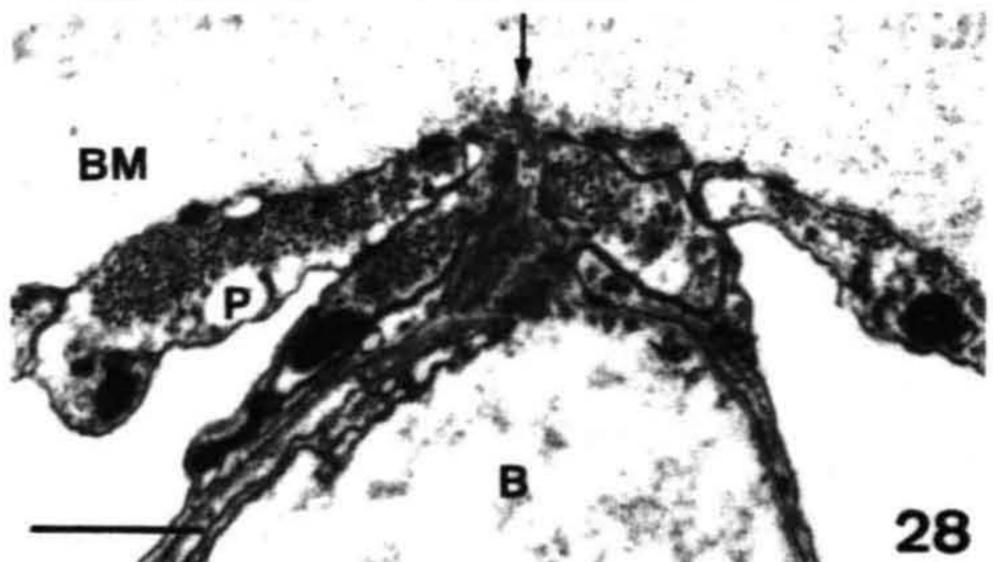
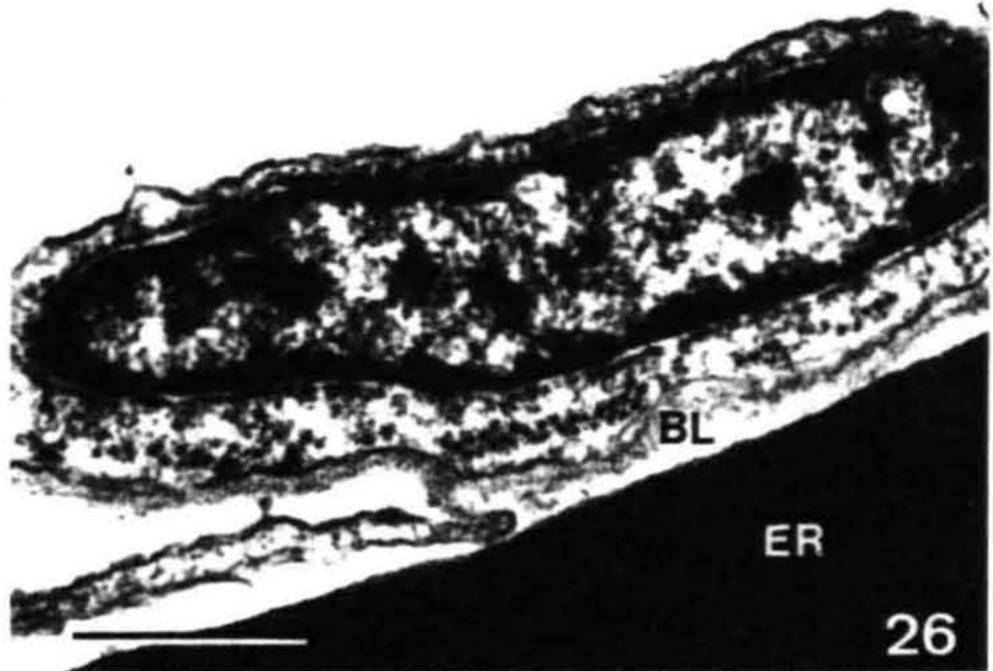
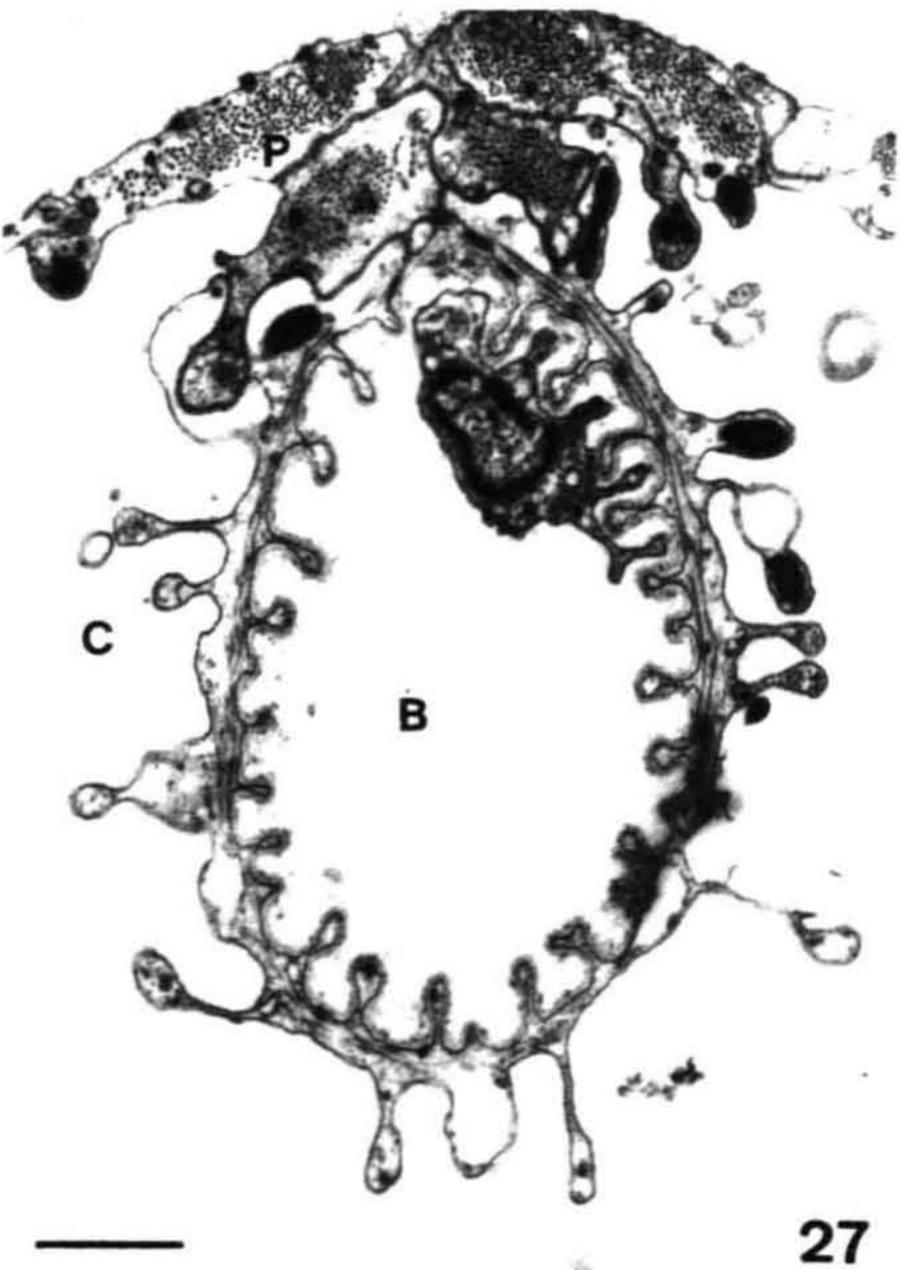
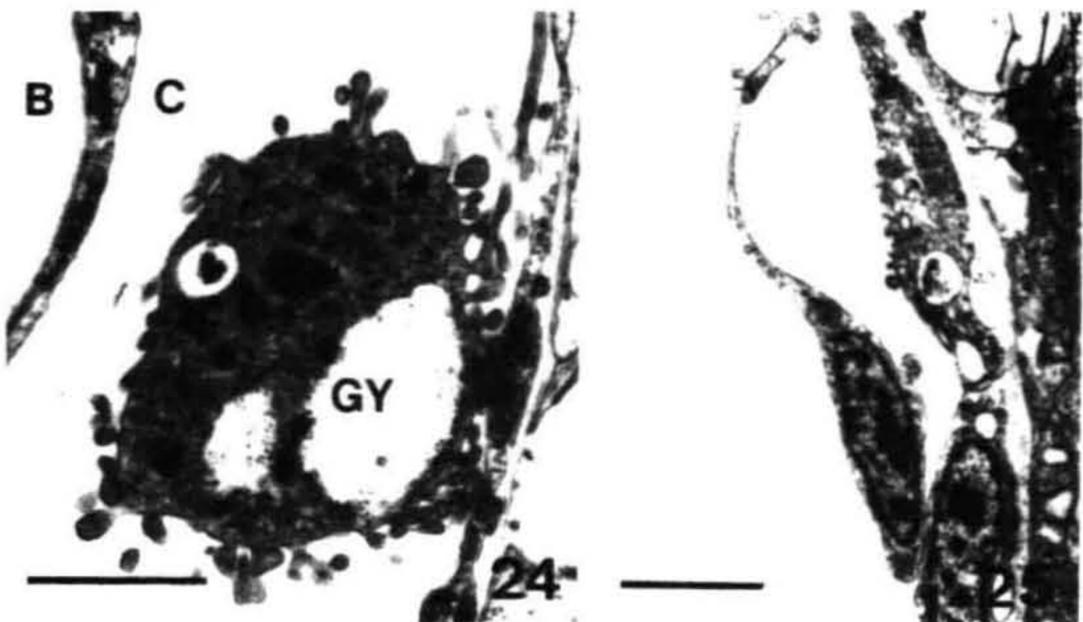
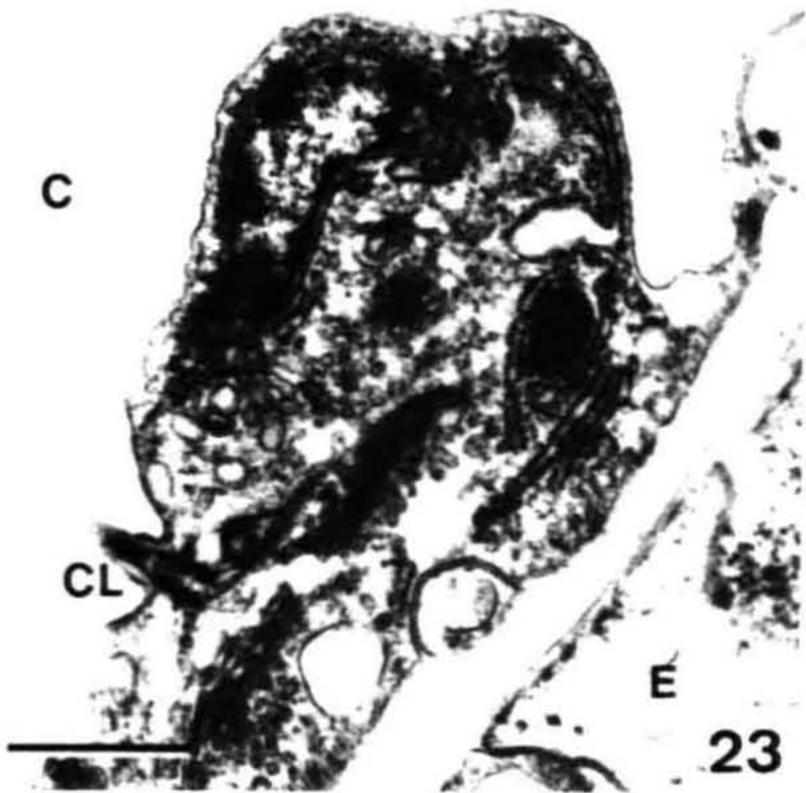
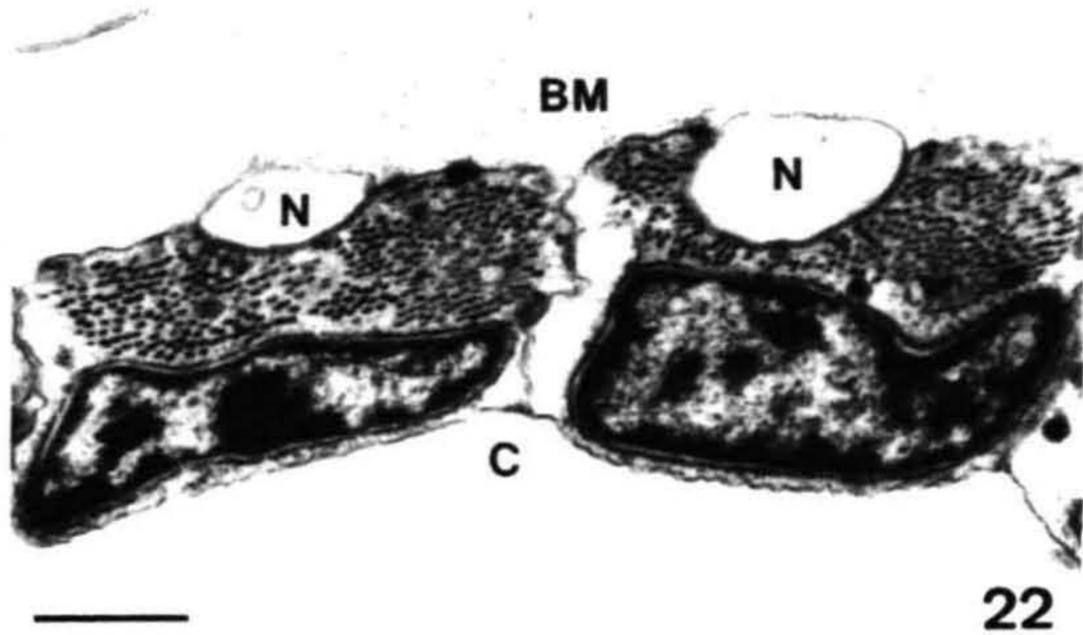
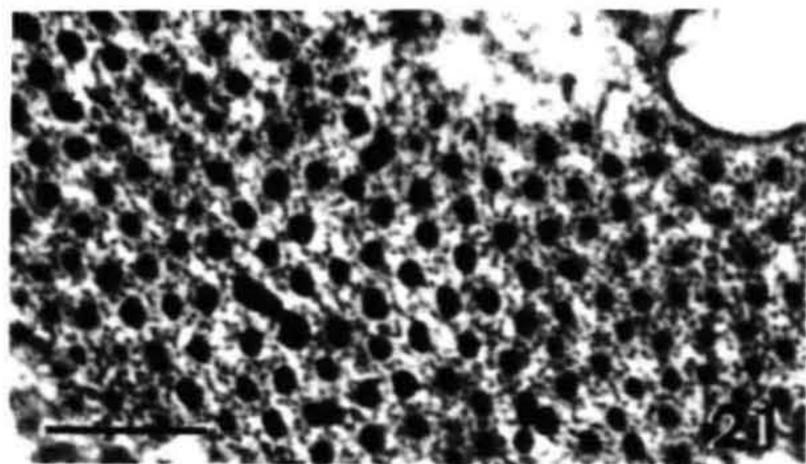
Within the capillary, two types of blood cells have been recorded: amoebocytes and erythrocytes. The amoebocytes are similar to the second cell type described above in the coelomic cavity: they are usually attached to the vessel walls by means of their pseudopodia, mainly near the attachment zone of the basement membrane; when the vessel contracts, the attached amoebocytes follow the folded pattern of the wall (Fig. 27). Their cytoplasm shows RER cisterns, Golgi apparatus and numerous multivesicular and residual bodies; centrioles with associated striated rootlets have sometimes been observed. The erythrocytes are numerous, showing rounded forms and grooves of variable depth. The cytoplasm is filled by the respiratory pigment, which appears homogeneous and strongly electron dense, and several inclusions. The rounded nucleus has high amounts of heterochromatin (Figs 2, 19).

Discussion

Our morphological observations and ultrastructural findings support and augment previous interpretations about functional morphology of the lophophore.

The epidermal cells of the tentacles are monociliated in *Phoronis australis* (except the secretory cells which do not bear cilia) as in *Actinotrocha branchiata* (the larva of *P. muelleri*, see Bartolomaeus 1987; Hay-Schmidt 1989) and in *P. ijimai* as described by Nielsen [1987; in contrast to Gilmour's (1978) report of multiciliated cells]. Similar monociliated epithelial cells are found also in the tentacles of Brachiopoda (Storch & Welsch 1976; Reed & Cloney 1977; Nielsen 1987) and of Pterobranchia (Dilly 1972; Dilly *et al.* 1986), whereas the epithelial cells are multiciliated in the Bryozoa which generally have a smaller number of cells in the ciliary bands (Lutaud 1973; Smith 1973; Gordon 1974).

The ciliary bands of the tentacles are the feeding organs in all the lophophorates (see also Bullivant 1968; Smith & Watabe 1971; Smith 1973; Lutaud 1973; Strathmann 1973, 1982; Emig 1982). The orientation of the cilia as revealed by their basal structures is related to their functions of current production and particle capture; similar orientations of the cilia have been reported from both larval and adult phoronids and brachiopods by Nielsen (1987) and Hay-Schmidt (1989). The frontal and abfrontal cilia beat towards the basis of the tentacle and the lateral cilia beat abfrontally. These orientations are mirrored by the orientation of the line secondary rootlet-basal foot: the secondary root reinforces the cilium anchorage and is opposite to the effective stroke, while the basal foot is in the direction of the working movement of the cilium. A similar functional orientation seems to occur in the



Figs 21-28.—*Fig. 21.* High magnification of cross-sectioned myofilaments. Scale bar $0.2 \mu\text{m}$.—*Fig. 22.* Two adjacent peritoneal cells at the frontal face. A longitudinal subperitoneal nervous axon underlines each cell. Scale bar $1 \mu\text{m}$.—*Fig. 23.* Myoperitoneal cell on the lateral face with its single cilium. Scale bar $1 \mu\text{m}$.—*Fig. 24.* Lymphocyte-like cell in the coelomic cavity. Scale bar $2 \mu\text{m}$.—*Fig. 25.* Amoebocyte-like cell. Scale bar $2 \mu\text{m}$.—*Fig. 26.* Detail of a peritoneal cell on a longitudinal section of the capillary wall. Note the myofilaments (circular) near the basal lamina. Scale bar $0.7 \mu\text{m}$.—*Fig. 27.* Cross-section in a contracted blood capillary. Note the blood amoebocyte adapting to the folded wall. Scale bar $1 \mu\text{m}$.—*Fig. 28.* Attachment of the blood capillary through its basal lamina to the tentacular basement membrane (*arrow*). Scale bar $1 \mu\text{m}$.

myoepithelial cells of the nephridial funnel in *P. muelleri* according to Bartolomaeus (1987, Fig. 19).

Within the lophophore of *P. australis*, the main water current created by the cilia runs along the frontal face of the tentacles towards the mouth (Figs 1, 7); the abfrontal face, with a decrease of the cilium density, plays a role which seems related to particle expelling rather than to current inducing.

The epidermis is protected from abrasion by the glyco-calyx and by the mucus secretion from the secretory A-cells. Some of the secretory cells could also have adhesive properties (i.e. for particle capture) because they resemble the adhesive cells in the Turbellarian epidermis (Tyler 1976, 1984); in Brachiopoda, a direct uptake of food particles has been suggested by Reed & Cloney (1977).

Frontolateral sensory cells facing the currents set up by the other cilia have been described previously in Phoronida and in Brachiopoda (Strathmann 1973; Gilmour 1978), in *Actinotrocha* (Hay-Schmidt 1989), in Bryozoa (Lutaud 1973; Gordon 1974), in Pterobranchia (Dilly 1972; Lester 1985; Dilly *et al.* 1986) and are believed to function in the feeding and protective mechanisms. The eight keel-shaped microvilli of the sensory cells in *Phoronis australis* are similar to those in the tentacles of *P. ijimai* (see Gilmour 1978) and in the larval tentacle of *Actinotrocha branchiata* in which the sensory cells show an unusual three-rooted cilium (Hay-Schmidt 1989). The direct putative synapses of the sensory cells with the basiepidermal nervous fibres suggest functions both in control and co-ordination of the ciliary beating and in food particle detection (as well as the recognition of food particles from inorganic material as pointed out by Gilmour 1978); the sensory cells probably also direct both smaller tentacle movements or the retraction of the animal into its tube according to the character of the disturbances.

The presence of myoepithelial cells in the tentacular peritoneum of Lophophorata is a usual feature, but a peritoneal lining composed exclusively of myoepithelial cells all around the tentacular coelomic canal has not been described previously. The peritoneal cells with the largest number of contractile fibrils are always located at the frontal face (where the basement membrane also has its largest thickness) in Phoronida, Bryozoa (Smith & Watabe 1971; Lutaud 1973; Smith 1973; Gordon 1974) and Brachiopoda (Storch & Welsch 1976; Reed & Cloney 1977; Reynolds & McCammon 1977), while cells with fewer myofilaments occur at the abfrontal face. In *P. australis* and in *A. branchiata*, all the myofibrils belong to the smooth type; in Brachiopoda (Reynolds & McCammon 1977) they are striated on the frontal face and smooth on the abfrontal face, and in Bryozoa (Smith 1973) they are all striated. In Phoronida, the myofilaments are oriented longitudinally all around the tentacle acting as tentacle 'muscles', most commonly bending the tentacle into the lophophoral cavity as the result of contraction of the main, frontal group of peritoneal cells. In the wall of the blood capillary, the myofilaments of the peritoneal cell are directed transversally, causing only peristaltic waves. The structure of the capillary wall is similar to that described in *P. psammophila* by Emig (1977), as in the

brachiopods *Lingula anatina* by Storch & Welsch (1976) and *Terebratalia transversa* by Reed & Cloney (1977). None of these forms have endothelia in the capillaries, which is considered the primitive condition (see Ruppert & Carle 1983).

The tentacular nervous system in *P. australis* consists of: two main basiepidermal groups of nervous bundles, those at the frontal face with the highest density of cilia and with the sensory cells being more conspicuous than those at the abfrontal face. A similar arrangement has been found in *A. branchiata* by Hay-Schmidt (1989). Among the other Lophophorata, the nerve bundles do not have determined locations in Bryozoa (Lutaud 1973; Smith 1973; Gordon 1974); in Brachiopoda, Reed & Cloney (1977) reported nerve fibres only at the frontal part of the tentacle of *Terebratalia*.

Single, longitudinal, subperitoneal axons under the epitheliomuscular cell are probably engaged in the control of the musculature. No nerve process has been observed crossing the basement membrane. In Bryozoa, Gordon (1974) found two lateral subperitoneal nerves in the tentacles of *Cryptosula pallasiana*, and Smith (1973) described nerve processes of subepidermal origin crossing the basement membrane in *Flustrellidra hispida*. Dilly (1972) observed some rare subperitoneal nerve profiles in the tentacles of the hemichordate *Rhabdopleura*.

Finally, the tentacles of *Phoronis australis* compared with the larval tentacles of *Actinotrocha branchiata*, have a similar arrangement of the epidermal cell layer, but differ fundamentally in the internal lumen organization (i.e. mesocoelomic structures). On the other hand the tentacles of *Phoronis australis* are more similar to brachiopod tentacles than to bryozoan ones.

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Abbreviations Used in Figures

A	amoebocyte
AF	abfrontal face of the tentacle
B	blood capillary
BF	basal foot
BL	basal lamina
BM	basement membrane
C	coelom
CL	cilium
D	dictyosome
DC	distal centriole
E	epidermis
ER	erythrocyte
F	frontal face of the tentacle
GY	glycogen
L	lateral face of the tentacle
M	mucous cell
MV	microvilli
MY	myofilaments
N	nerve fibres
P	peritoneum
PC	proximal centriole
R	rootlet
RER	rough endoplasmic reticulum

S	secretory granule
Sc	secretory cell
SR	secondary rootlet

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